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Restoration of historical and novel vegetation in Central Europe

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Abstract

Restoration ecology is rich in theoretical concepts and aims at developing widely applicable solutions for degraded ecosystems. In recent years it has been recognised that ecological restoration has to take into account historical contingencies in land use that differ among continents and regions. Here we give a short overview on current directions of restoration ecology, contrasting near-natural, semi-natural and 'novel ecosystems', with special reference to the relative importance of archaeo- and neobiota in Central European grasslands. We contend that too little is known about species assembly and ecosystem function in novel ecosystems, and in fact about the degree of novelty in European ecosystems, to accept them as future landscape elements without hesitation. On the other hand, the precautionary focus on historical species assemblages and distribution ranges in restoration is costly and may prove a too rigid framework under future environmental change. Systematic hypothesis testing using 'adaptive restoration' seems a promising approach to deal with these challenges, especially in heavily degraded ecosystems and in periods of rapid and unpredictable environmental change.

Zusammenfassung

Dieser Artikel beschreibt die Relevanz aktueller Konzepte der Renaturierungsökologie im Kontext zentraleuropäischer Ökosysteme, insbesondere mit Hinblick auf Artengemeinschaften, die in vor- und nachkolumbianischer Zeit entstanden sind. Zur Entwicklung und nachhaltigen Funktionsfähigkeit dieser neuartigen Ökoysteme (‚novel ecosystems') bestehen noch große Wissenslücken. Um diese Lücken zu schließen und auch schwierig vorhersagbaren Umweltveränderungen Rechnung zu tragen, wird empfohlen, Renaturierung nicht ausschließlich nach dem Vorsorgeprinzip und mit kostenintensivsten Methoden zu betreiben, sondern Freiraum für systematische Überprüfung von Hypothesen und langfristige Beobachtungsreihen im Rahmen eines adaptiven Ansatzes zu lassen.

1. Introduction

Despite considerable efforts in nature conservation and ecological restoration during the past 50 years, the overwhelming current trend appears to be man-mediated alteration and destruction of habitats. Although recovery of formerly endangered species and communities has been successful in a variety of cases, the overall negative trend in biodiversity is far from changed. The European Commission emphasises the following major threats to plant species and communities: Habitat loss and degradation, introduction of invasive non-native species, pollution and disease, and climate change (SILVA et al. 2008). Similar trends are observed in most industrialised countries (http://www.iucn.org/).

In order to improve this unfortunate situation, governments give incentives to support biological conservation and connect habitat fragments by restoration of degraded habitats. The science and practice of restoration have developed considerably since the 1960s, and most industrialised countries already dispose of a wealth of restoration techniques, including commercialised seed production of wild genotypes of native species. Initially, the aim of ecological restoration was the restitution of more or less subjectively chosen states and properties that ecosystems presumably had prior to human intervention (CLEWELL & ARONSON 2007). The historical role of humans in creation of diverse plant communities has since then been acknowledged by inclusion of 'cultural ecosystems' as possible targets of restoration in the SER Primer (2004).

In future, ecological restoration may become even more sophisticated and more expensive. At the same time, the recent 'novel ecosystems' debate reveals increasing doubts as to whether restoration at all costs is always justifiable. This debate is focused on the ecological functions and services of man-made ecosystems resulting from formation of new habitat conditions and introduction of non-native species. Well-known examples of new ecosystem types in Europe are ruderalised urban woodlands or regulated rivers with abundant biological invasions. The relative importance and conservation value of native and non-native species do need more attention, and results from such research may lead to a paradigm shift in conservation and restoration (cf. HERMANN et al. 2013).

Central European restoration ecologists have not joined in the novel ecosystems debate to similar extent as their colleagues from the Americas and Australia, perhaps because ecological restoration in Central Europe has since decades been directed by the long cultural history of land use with highly diverse landscapes and vegetation types that have been intensively studied. However, it is this peculiar position from which valuable input for future directions of restoration and novel ecosystems ecology can be given.

2. Restoration ecology: A brief glossary

Any newcomer to ecological restoration must first find their way through a maze of terms that are applied to this science and its respective practice. This exercise is, however, worthwhile, because the terms differ not only according to the starting conditions of degraded ecosystems, but also according to the goals to be reached, and the financial and technical resources invested. This again has implications for the novel ecosystems debate. In the following, some of the terms of ecological restoration are outlined and discussed in order to highlight the major contrasts. Figure 1 shows two contrasting starting conditions for the several types of restoration s.l.; a more extensive overview in German language is provided by ZERBE et al. (2009).

Recultivation or *reclamation* takes place when wastelands, a result of mining, peat extraction, poor ecosystem management and desertification, are actively developed to support once more agricultural land use, horticulture, forestry or recreation. While this approach tends more towards restoring normal ('higher') soil functioning and productivity (HIGGS 2003), the term *reconstruction* was coined by BRADSHAW (1984) for the active acceleration of processes that would occur in the course of primary succession on the raw substrates in a post-mining landscape, and result in a functioning, self-sustaining ecosystem, although not necessarily consisting of the same species that populated the site prior to destruction (Fig 1A).

Revitalisation, rehabilitation, and – more recently – *intervention* usually take place in communities where some developed soil and vegetation is present, however far degraded. *Revitalisation* involves improvement of habitat conditions (‘abiotic conditions’ according to ZERBE et al. 2009) to encourage recolonisation by plant and animal species; the term is frequently applied in river restoration, when water quality is improved and flow dynamics are once more increased. *Rehabilitation* has been variously defined as alteration of “damaging practices” (HIGGS 2003), as “isolated manipulation of individual ecosystem elements to a less degraded state” (SIMENSTAD et al. 2006) or even as “restoring specific ecosystem functions rather than original ecosystem components” (CHOI 2007). The latter, at least, also implies that the species providing function are not necessarily the same as prior to site degradation. They might even be non-native species (Fig. 1B).

Ecological restoration s.s. is the core concept of the world-wide operating Society for Ecological Restoration (SER) and thus, this term has been most elaborately discussed and re-formulated in the past decade. It is “the process of assisting the recovery of an impaired ecosystem to a desired condition” in which the desired condition includes ecological functioning, self-organisation, the capacity for self-sustainability (CLEWELL & ARONSON 2007). The restored ecosystem should consist “of indigenous species to the greatest practicable extent” (SER 2004), although “allowances can be made” for non-invasive, exotic or domesticated species and co-evolved ruderal and segetal species if the system is a “cultural system” in SER terminology.

The common aim of all approaches is to move the system towards a state in which biodiversity and ecosystem functions are higher than in the degraded state. If the starting condition

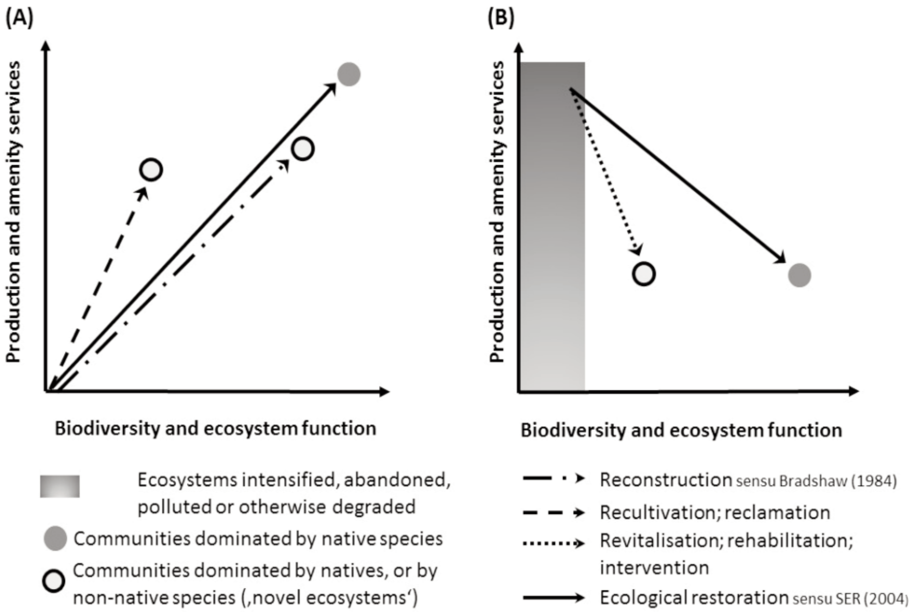

Fig. 1: A synthesis of restoration approaches and outcomes. Destroyed or severely degraded sites, left e.g. after mining or peat extraction, are the starting point in graph (A). The starting point in graph (B) are systems with developed soil, vegetation and seed bank, although degraded and impoverished, as often observed in cultural landscapes after intensive agricultural land use. Only selected trajectories are shown; for details see text.

is a wasteland lacking even substrates for growth, i.e. biodiversity as well as production and amenity services are practically zero, then active development will also necessarily move the system towards better provisioning of services (Fig. 1A). However, in industrialised countries, where land-use intensification has provoked major losses in biodiversity and ecosystem functions, restoration often has to aim at decreasing habitat productivity as a prerequisite to increase species richness (Fig. 1B).

Recently, controversy has arisen about what species may constitute restored biodiversity. Ecological restoration is, arguably, the most demanding of all approaches to restoration. Yet, as reported above, SER (2004) includes a waiver on non-native (albeit non-invasive!) species and genotypes. This is a remarkable approach in times when potential invasiveness of deliberately and inadvertently introduced non-native species fills books, journals and conferences. In the following two sections we explore this ambiguity with reference to Central European ecosystems, especially grasslands, because their history and community types are particularly well known.

3. Non-native species and novel ecosystems: Friends or foes?

Central European vegetation has been shaped by humans and associated livestock since the Neolithic period. Clear-cutting and grazing first turned natural forests into park-like landscapes in which tree regeneration was suppressed and grassland communities assembled spontaneously from the regional species pool (ELLENBERG & LEUSCHNER 2010). As the Neolithic population colonised Middle Europe from the southeast, so did species from Eurasian temperate steppes find their way into these regional species pools. The earliest arable fields, in which man-mediated plant introductions were a core component, also harboured rich herb communities and were used for livestock grazing (IBID.).

These semi-natural communities and their key species are nowadays protected by nature conservation laws in the member states of the European Union (COUNCIL DIRECTIVE 92/43/EEC of 21 May 1992), having become severely threatened, once more by human action, in the wake of the industrial revolution and globalisation of trade. It is consensus among European restoration ecologists that they are a worthy aim of restoration, and suitable techniques have been advocated in several comprehensive publications (KIRMER & TISCHEW 2006, KIEHL et al. 2014).

The SER Primer (2004) refers, however, to ‘exotic’ species, which seems to anticipate a more controversial concept introduced to restoration ecologists in 2006: It is the idea of novel ecosystems replacing, at least in some areas, natural ecosystems (HOBBS et al. 2006). What are novel ecosystems? – According to a recent working definition, a novel ecosystem “is a system of abiotic, biotic and social components … that, by virtue of human influence, differ from those that prevailed historically, having a tendency to self-organise and manifest novel qualities without intensive human management” (HOBBS et al. 2013a). This definition is broad enough to accommodate a variety of the abovementioned European pasture grasslands and fodder meadows; but these are not what the novel ecosystems concept is applied to! In fact, seven out of eight case studies reported in HOBBS et al. (2013b) deal with post-Columbian introduced plants, colonising sites that result from post-Columbian exploitation and trading of natural resources.

Novel ecosystems are, in other words, products of an era in which species were no longer transferred largely within but rather among continents. The turning point, illustrated in Fig. 2, came around 1500 AD with discovery and colonisation of the Americas by Europeans. Australia was the final continent to be included in regular transoceanic shipping routes, approximately two centuries ago. These last two decades were also marked by environmental changes at unprecedented speed, following industrialisation and the expansion of global trade since 1800.

Species transport between Europe, America, southern Africa and Australia occurred both deliberately and inadvertently. Most prominent among deliberate exports from Europe were crops, fodder grasses and herbs, along with introduction of livestock and European grassland management (haymaking) into novel ranges wherever site conditions permitted. Most prominent among deliberate imports into Europe were Northern American trees, shrubs and prairie forbs for silvi- and horticulture and landscaping.

German ecologists customarily refer to pre-Columbian introductions as 'archaeo'-biota and to post-Columbian introductions as 'neo'-biota for distinction. The term 'invasive' is applied to neobiota (never to archaeobiota) that not only establish and reproduce in a novel range but spread so excessively that biodiversity is reduced, and ecosystem functions and dynamics are significantly altered. There is no conclusive answer to which combination of traits and environmental conditions promote invasiveness. However, there is, for example, strong evidence that invasiveness of European species globally is connected to high relative growth rates, which may have been selected for both under long-term management in the home range, and during introduction into novel ranges (DAWSON et al. 2011); MACK (2000) argued that widespread cultivation and sowing increases probability of naturalisation even in such species that initially depend on human care for maintenance of their introduced populations. The all-pervading influence of man even in remote areas is increasingly being recognised.

In some of the recently reported cases on novel ecosystems, neobiota have mixed with native species inconspicuously, or even benefitted native species (SCHLÄPFER et al. 2011 and references therein). In others, they have spread excessively, to the detriment of biodiversity, but have resisted all but the most radical attempts at restoration (e.g. EWEL 2013). These phenomena have prompted restoration ecologists to question the validity of historic ecosystem states as a restoration goal and to "embrace novelty" and the systems that may develop from introduced species.

The novel ecosystems concept has not been broadly adopted in European restoration ecology. Judging by the fact that merely four of fifty contributors to HOBBS et al. (2013b) are based in the UK and none in continental Europe, while 38 came from the US, Canada or Australia, it does not even seem to be of great interest. Why is this so? – Firstly, much of the novel ecosystem controversy revolves around the question whether they can develop into systems with high diversity and multiple functions (as European semi-natural ecosystems did), and if so, under which environmental conditions, and over which timespan.

It is crucial, in order to answer this question, to develop distinct assembly rules for species communities developed in pre- and post-industrialization times, from pre-Colombian and post-Colombian introduced species (archaeo- and neobiota, respectively), from wild genotypes and cultivated varieties. The MEND experiment in Texas (WILSEY et al. 2009) is a prime example for such an approach. Secondly, given the timespan it took semi-natural communities to develop (Fig. 2), and the considerable rates of species loss currently reported, it may not be that restoration ecologists will live to witness assembly of highly diverse, selforganising novel communities in Europe. This is an understandable motive for turning to well-known historical communities that used to characterise the project area. Finally, as will be shown in the following section, the degree of post-Colombian novelty in European ecosystems is far from fully known.

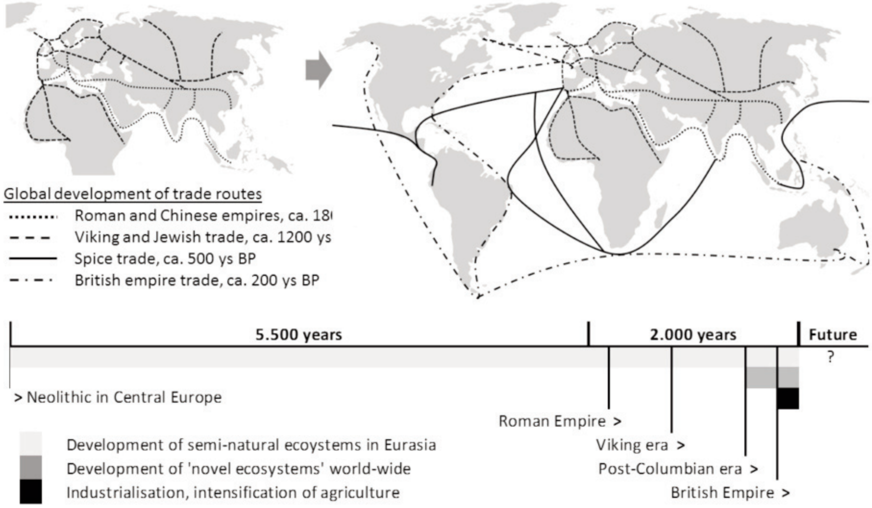

Fig. 2: A comparison of the spatial and temporal scale over which two groups of ecosystems became established. Semi-natural ecosystems, especially pastures and meadows, have developed over thousands of years from a species pool largely restricted to the Eurasian continent (top left). Novel ecosystems, on the other hand, have developed from plant and animal species transferred across and between continents in the post-Columbian era. Their nature conservation value and evolutionary potential are controversial in restoration ecology.

4. Novelty in European grasslands

What happened to the European semi-natural communities in the era of novelty, and what are the implications for contemporary restoration? – From the viewpoint of nature conservation today, developments were both positive and (mostly) negative. The diversification of grassland types was positive. Artificial grasslands were seeded in Central Europe, to supply winter fodder for livestock, since Roman times (ELLENBERG & LEUSCHNER 2010) and especially since the beginning of the 19th century (KAUTER et al. 2002). The intensification of grassland management had more negative consequences. At least part of the seeded grasslands were regularly fertilised and cut more than once per growing season even before the invention of synthetic fertiliser (KAUTER et al. 2002), which would have selected for fast- and tall-growing species. Nutrient loads increased heavily from 1850 onwards with the invention of artificial fertiliser.

Towards the end of the 19th century, when cheap wool exports from New Zealand made sheep farming in Middle Europe unprofitable, large tracts of semi-natural grasslands were abandoned and often converted to arable land and forest plantations. Cultivation of artificial pastures, on the other hand, boomed around 1880, following a crash in corn prices (SHEAIL 1986). Systematic breeding of productive forage grasses increased. Global markets were already so well developed that at least until the 1920s much of the grass and legume seed required in Europe was propagated in the United States (WALKER et al. 2004) – where, incidentally, cultivars of Eurasian origin were liberally seeded. The past decades, in Europe, have seen a steadily increasing intensity of land use in the form of site melioration, larger fields and frequent application of fertilisers and pesticides. This has resulted in a steep decline in diversity of plant communities and species.

Remnants of semi-natural grasslands continue to be endangered, and even restoration attempts may be futile, in contemporary landscapes. First, as these communities consist mostly of long-lived specialists that are slow in responding to habitat fragmentation, it is feared that remnant communities will decline in species numbers even if habitat size is not further reduced (KRAUSS et al. 2010). This is a clear case of extinction debt. Second, re-introduction of management in abandoned grasslands is often not sufficient to restore former species diversity, because many grassland plant species do not have persistent seed banks and dispersal distances of only a few (dozen) metres (STAMPFLI & ZEITER 1991; BAKKER & BERENDSE 1999). Third, critical nitrogen loads for grasslands on formerly nutrient-poor soils, as listed by BAKKER & BERENDSE (1999), are nowadays in some regions of Central Europe surpassed by airborne input alone (cf. DUPRÈ et al. 2010). And fourth, climate change may affect in particular grassland communities in mountain ranges, although observations point to a stronger impact on subnival pioneer than on alpine grassland communities (e.g. VITTOZ et al. 2009).

At least in terms of grassland species invasion, Central Europe has, at first glance, dished out more than taken. More than half of the grass varieties listed by HANSON (1959) for the United States were derived from introduced Eurasian C_3 species (as opposed to less than 10% from native American C_3 species). Several of these species have become invasive in prairie remnants, e.g. *Poa pratensis* and *Bromus inermis* (CULLY et al. 2003). Grass and herb species exported both deliberately and accidentally, have modified entire regions of the United States and Australia. This is hardly surprising given the historical and present-day extent of human selection, propagation and seeding. On the other hand, reports on invasive neophytes in calcareous grasslands, fenlands, Arrhenatheretum meadows in Europe are comparatively scarce. Although several American prairie species, introduced as garden ornamentals, have naturalised and some have spread aggressively – most notoriously, *Erigeron annuus, Solidago canadensis* and *S. gigantea* – these species are mostly restricted to somehow ruderalised sites. It may be hypothesised that the long history of grassland use and cultivation in Europe has contributed to the invasion-resistance of species assemblages composed of natives and archaeophytes.

In the wake of global marketing of grassland species, however, more cryptic invasions are taking place in Central Europe, or are feared to have done so. Rapid emergence of subspecies in novel ranges, one of the most controversial being *Festuca rubra* ssp. *commutata*, has been linked to broad-scale introduction by grass seed mixes (WALKER et al. 2004). Introgression of novel genotypes, through cultivars and wildflower seed propagated abroad, is feared to either reduce fitness (loss of local adaptation), or increase fitness (heterosis) so that less competitive native species and genotypes are suppressed. Experimental evidence on these hypotheses is equivocal (e.g. SCHRÖDER & PRASSE 2013, WALKER et al. 2015). Only in the following years, with the development of lower-priced molecular analysis, researchers might be able to quantify the extent of novel genetic assemblages in European grasslands, and obtain conclusive evidence on the feedbacks on ecosystem diversity and functioning.

5. Ways for ecological restoration in Central Europe

"… I made the remark that 'The only way to restore the native wet prairies would be to come in here with bulldozers and cart that Anthrosol out'… 17 years after … the Park was undertaking Hole-in-the-Donut restoration by removing the anthrosol. I was incredulous." (EWEL 2013) – The quotation in the beginning of this chapter refers to a US restoration site in Florida invaded by (formerly ornamental) southern American *Schinus* trees. However, all of the highly industrialised countries of Central Europe favour technically refined 'cookbook restoration' of strictly defined, historically present ecosystem types.

Low-cost restoration by spontaneous succession is still a common approach in southeast Europe, e.g. Romania (RUPRECHT 2006) and the Czech Republic (LENCOVÁ & PRACH 2011), but will only result in mostly native communities if large remnants still exist close to the restoration site. In continental Middle Europe and the U.K., target species are often transferred by hay or seed mixes (HEDBERG & KOTOWSKI 2010), with seed sourcing for mixes being increasingly regulated. In its most extreme form, in spite of presently contradictory results, German legislation now promotes seed sourcing, propagation and use for restoration purposes according to eight pre-defined origin zones, in order to preserve local gene pools besides species assemblages (RIEGER et al. 2014). Concomitant with this development, the deliberate use of non-local genotypes, non-native genotypes or even species is a taboo, or at least frowned upon in nature conservation and restoration circles. Incentives to employ mixtures of local and non-local genotypes in unpredictable settings (e.g. BROADHURST et al. 2008) and to select genotypes to perform well in ecological restoration (JONES 2013) are again restricted to Anglo-American countries.

It is the responsibility of restoration and of nature conservation to ensure that ecosystems resist invasion now and in future decades, under continuous influx of non-native species and global warming, to name two of the most drastic and poorly predictable changes. While it is true that grass and legume varieties selected for high competitive ability have been used too uncritically in landscape and restoration settings, impairing species diversity (e.g. CONRAD & TISCHEW 2011), strict confinement of seed sourcing to locally sourced (putatively) wild genotypes denies a long history of interaction between man and nature in Europe, and may consolidate a status quo that is not sustainable in the long term.

It may be wise to invest, besides technical refinement of site preparation and species transfer, in multifactorial experimental approaches in restoration and long-term monitoring of both manipulated and un-manipulated sites. Approaching uncertainties in ecosystem development by experimentation was first proposed by HOLLING (1978) as 'adaptive management', meant to improve environmental management in an iterative process of testing and evaluating management approaches (Fig. 3A). More recently, ZEDLER & KERCHER (2005) suggested 'adaptive restoration' to allow for modification of management and restoration methods in the case of unforeseen developments, while the objective is still improvement of a degraded site, and the target ecosystem is pre-defined (Fig. 3B and C). The adaptive restoration concept has received world-wide attention, although relevant publications originate mostly from the US, and from studies on aquatic and semi-aquatic habitats, in which context it was originally proposed. We contend it is a good incentive to introduce flexibility in methods and scientific rigour into a greater number of restoration sites in Europe, and to improve, at the same time, our knowledge about development of novel communities, without betraying the values of ecological restoration.

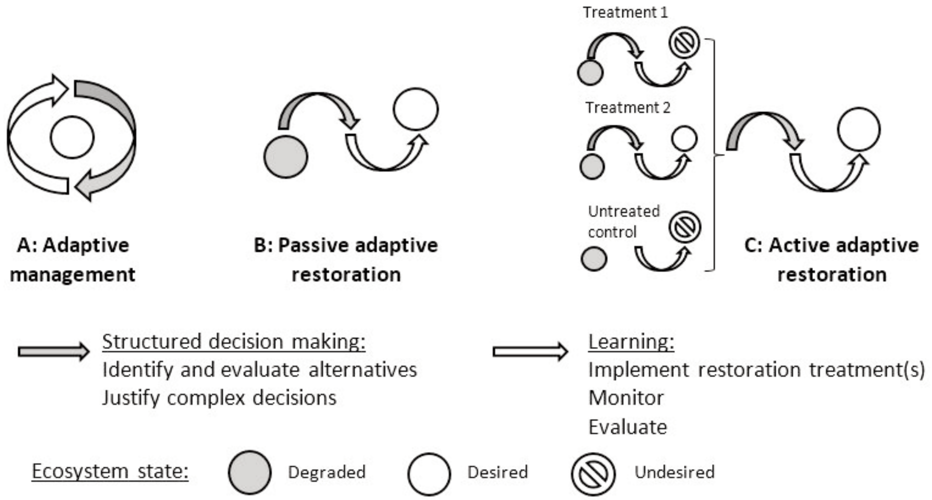

Fig. 3: Adaptive restoration repeatedly goes through a decision making and a learning phase until a degraded ecosystem has developed to a desired state. Restoration is 'passively adaptive' if subsequently refined on the basis of monitoring, and 'actively adaptive' if parallel hypothesis testing occurs in subsets of the area.

6. Conclusions

There are universal principles in ecological restoration, but they need to be regionally differentiated. For Central Europe we recommend continued efforts in restoring natural communities in sites where human land use never has played a dominating role, as for example in national parks. Historical plant communities that were adapted to nutrient-poor site conditions and specific methods of the cultural landscape should be restored where this still is feasible. This may require new methods of integrating biodiversity into the current socio-economic framework of farming. Finally, in sites that have been drastically changed by pollution, soil degradation and invasive species, creation of novel ecosystems might be the most promising approach; other than outside Europe, novelty may consist in novel genetic rather than species assemblages. Adaptive restoration would allow both for new scientific insights, a higher flexibility in practice, and increasing biodiversity at the landscape scale corresponding to the diversity of complementary methods applied. Last but not least, adaptive restoration might stimulate a productive dialogue between scientists, restoration practitioners and the various land users.

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